

Taxonomic tangles posed by human association – the urgent need for an evidence-based review of dingo and domestic dog taxonomy and nomenclature

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ABSTRACT

A serious challenge in modern taxonomy is whether, or how, relationships with humans have altered the evolutionary trajectory of species and how this should be dealt with in taxonomic nomenclature. Despite their historic treatment as a discrete taxon, the taxonomy and nomenclature of dingoes has been robustly debated for decades, in part due to their close evolutionary relationship to wolves and domestic dogs, as well as uncertainty about the role of humans in shaping their origins. One outcome of this ongoing scientific debate is a set of criteria regarding reproductive isolation, evolutionary distinctiveness and evolutionary origins that can be used to refine discussion about the appropriate taxonomy of dingoes. We review significant scientific advances in our knowledge of the distinct identity of dingoes in light of these criteria and discuss the need for scientists to assess the multi-stage process of domestication when considering species that may have interacted with humans over evolutionary timescales. Current evidence indicates that dingoes are on a different evolutionary trajectory to domestic dogs and thus we argue that the appropriate nomenclature for dingoes is *Canis dingo* or *Canis lupus dingo*, not *Canis familiaris*. We suggest that an independent evidence-based scientific review with expert consultation is one pathway through which taxonomic debate about dingoes and other controversial species could be resolved.

Keywords: *Canis dingo*, *Canis familiaris*, *Canis lupus dingo*, culturally significant species/entity, dingo, domestic dog, taxonomic nomenclature.

Introduction

Species concepts are a theoretical framework by which scientists attempt to classify and organise Earth's biodiversity (Zachos 2016). A great challenge for modern taxonomy is how to deal with species or animal lineages that have complex evolutionary histories, or may have been associated with humans over time (Gentry *et al.* 2004; Clutton-Brock 2015). Here we use the term 'association' to describe a continuum of geographic co-occurrence and interaction between animal populations and humans that may or may not lead to domestication. This is because the intensity and occurrence of interactions with humans can, over long periods of time, lead to differences in morphology, behaviour or ecology between associated and non-associated or 'wild' animals. This is relevant to how we define a domestic lineage and whether domestic lineages, especially those that are genetically and morphologically distinct from their wild relatives, should be classed as separate species or excluded from taxonomic nomenclature (Clutton-Brock 1992; Gentry *et al.* 2004; Clutton-Brock 2015; Jackson *et al.* 2017; Zeller and Göttert 2019). It is therefore critical that scientists considering the taxonomic nomenclature of wild and domestic lineages use an accepted definition of domestication (Zeder 2012; Larson and Burger 2013; Lord *et al.* 2025).

It is currently common practice for lineages falling within the wild to domestic continuum to be distinguished using binomial taxonomic nomenclature (Gentry *et al.* 2004).

This is reflected in International Commission on Zoological Nomenclature (ICZN) Opinion 2027 which allows ‘... taxonomic judgement as to what degree of domestication can be encompassed in the species-concept ...’ (Gentry *et al.* 2004, p. 649). Distinguishing wild and domestic lineages is important to reflect differing evolutionary trajectories. Whilst some taxonomists hold the opinion that lineages associated with humans cannot speciate (Jackson *et al.* 2017; Zeller and Göttert 2019), this arbitrarily disregards the role natural selection plays in shaping lineages, especially those that may have had associations with humans but no deliberate artificial selection. It is also problematic to apply such ideas universally, given the complex relationships different peoples, including Indigenous peoples, have had and maintain with certain animals over millennia (Smith and Litchfield 2009; Fogg *et al.* 2015). For instance, Indigenous Australians connect to Country through a network of relationships which include kinship with Culturally Significant Species (Goolmeier *et al.* 2022). These linkages include very close relationships with *Canis* species which lived, and still live, entwined with those of Indigenous communities. Many indigenous languages have two words for *Canis* species that make a distinction between wild and human associated animals. Using nomenclature to differentiate between domestic and wild lineages also provides clarity to policy makers needing to conserve wildlife or identify illegal imports or exports of an endangered wild versus domestic species (Gentry *et al.* 2004; Clutton-Brock 2015; Zeller and Göttert 2019). In addition, what we call a species has conservation implications, particularly where classification embeds a taxon as a subspecies within common or widespread species with discordant management strategies, or where the taxonomic nomenclature may inappropriately preclude a lineage from legislative protection (Ritchie *et al.* 2018; vonHoldt *et al.* 2018).

Historically dingoes have been identified as a discrete taxon from domestic dogs, with three different species names in current widespread use (Crowther *et al.* 2014; Smith *et al.* 2019). In this paper, we focus on the evidence and knowledge gaps underlying debate on the taxonomy and nomenclature of dingoes and outline the consequences of taxonomic uncertainty for conservation policy. The three most common taxonomic names applied to dingoes over the last 30 years are: *Canis lupus dingo* (a subspecies of wolf), *Canis dingo* (a distinct species) and *Canis familiaris* (a domestic dog) (Daniels and Corbett 2003; Sillero-Zubiri 2009; Crowther *et al.* 2014; Allen *et al.* 2017; Jackson *et al.* 2017; Smith *et al.* 2019; Jackson *et al.* 2020; Cairns 2021; Shipman 2021; Krofel *et al.* 2022). The main points of difference in the use of these names revolve around the level of reproductive isolation between dingoes and domestic dogs, whether dingoes are distinct from wolves or extant domestic dogs and whether the ancestor of dingoes was domesticated, which some suggest precludes them from being considered a distinct taxon (Jackson *et al.* 2017).

With new scientific knowledge about the evolutionary and contemporary identity of dingoes, we suggest a pathway

for resolving taxonomic debate about dingoes, which applies to other controversial species as well.

Background context: evolution of dogs

The evolution of dogs began approximately 20,000–40,000 years BP (Botigué *et al.* 2017; Freedman and Wayne 2017; Bergström *et al.* 2020). Current scientific knowledge suggests that rather than evolving directly from modern wolves, dogs evolved from either a common ancestor of the Holarctic wolf (Druzhkova *et al.* 2013; Thalmann *et al.* 2013; Freedman *et al.* 2014; Fan 2016; Freedman and Wayne 2017; Oetjens *et al.* 2018; Bergström *et al.* 2020; Perri *et al.* 2021; Gojobori *et al.* 2024) or originated directly from multiple geographically discrete grey wolf populations (Frantz *et al.* 2016; Freedman and Wayne 2017; Bergström *et al.* 2022). The exact nature and role of the relationship between early dogs and humans remains unclear. Within the *Canis* species complex, admixture between different *Canis*, and canid, lineages is common and may be adaptive (Sacks *et al.* 2013; vonHoldt *et al.* 2013; Skoglund *et al.* 2015; Fan *et al.* 2016; Frantz *et al.* 2016; Gopalakrishnan *et al.* 2018; Bergström *et al.* 2022; Gojobori *et al.* 2024). The diversification of early dogs into domestic dogs has been characterised by several periods of strong artificial selection, significantly predating and including during the transition of some human cultures to an agrarian lifestyle around 12,000 years ago (~10,000 BC) (Axelsson *et al.* 2013; Arendt *et al.* 2016; Cagan and Blass 2016; Freedman *et al.* 2016; Pendleton *et al.* 2018; Perri *et al.* 2021), and intensive selective breeding during modern breed formation around 200–500 years ago (vonHoldt *et al.* 2010; Parker *et al.* 2017).

It is important not to conflate the original divergence of wolves and dogs within the genus *Canis* with domestication because: (1) these processes may not have occurred simultaneously; (2) may not have been originally human-directed; and (3) domestication itself is a multi-stage, fluid and long-term process (Zeder 2012; Larson and Burger 2013). Dogs are commonly posited to have become domesticated through a commensal pathway (Fig. 1) characterised by a slowly intensifying relationship with humans; progressing from anthropophilic to commensal to controlled breeding to companion animal (Driscoll *et al.* 2009; Zeder 2012; Larson and Burger 2013; Marshall *et al.* 2014; Zeller and Göttert 2019). Anthropophilic or commensal associations with humans, particularly if there is no or limited control of breeding, are rarely included in definitions of domestication (Lord *et al.* 2025). A key feature that most definitions of domestication rely upon is controlled and intensive breeding by humans following an intensification of the animal-human relationship. A new definition proposed by Lord *et al.* (2025) suggests domestic ‘should refer solely to those populations that are obligate synanthropes’ and are unable to form self-sustaining populations outside of anthropogenic niches.

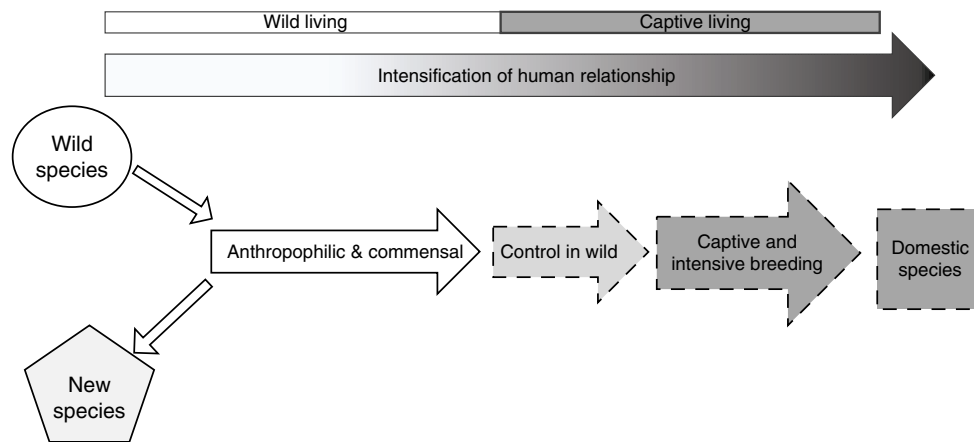


Fig. 1. Schematic of the ‘commensal’ domestication pathway originally hypothesised by [Larson and Burger \(2013\)](#) illustrating the intensification of the relationship with humans and changing relative strength of natural evolutionary forces. Solid lines indicate species or processes where natural evolutionary forces are occurring with limited impact of human selection on the lineage. Dashed lines indicate an increased impact and extent of human selection on the lineage to the exclusion of natural forces.

Resolving debate about the taxonomy of dingoes

Debate concerning the taxonomy and appropriate nomenclature for dingoes in Australia led [Jackson *et al.* \(2020, p. 352\)](#) to propose that one or more of the following conditions would need to be met for the dingo to be regarded a separate species:

1. New evidence of effective reproductive isolation of the dingo from related canids,
2. New genetic evidence that shows the dingo does not cluster within the diversity represented by domestic dog breeds,
3. New evidence that the dingo is an independently derived evolutionary lineage that is more distinct from domestic dog breeds, than these breeds are from each other,
4. In addition, the relationship of the Australian dingo population with other ‘dingo’ populations in mainland and island South-East Asia including New Guinea (Singing Dog) would need to be clarified.

Below, we demonstrate that there are multiple lines of evidence in support of these four criteria, and thus argue that dingoes should be considered a distinct taxonomic unit to domestic dogs, with discrete nomenclature. Whilst debate about taxonomic nomenclature is largely philosophical, it is important to note that nomenclature has a significant impact on the conservation and management of fauna and flora ([Ritchie *et al.* 2018](#)). Treatment of dingoes as a discrete species or sub-species enables governments to differentiate between dingoes and domestic dogs, allowing dingoes to be specifically protected or even listed as a threatened animal taxon. Nomenclature which does not distinguish between

dingoes and domestic dogs constrains conservation and management efforts, effectively grouping dingoes with domestic dogs as the same entity.

Criterion 1: evidence of effective reproductive isolation

Molecular dating efforts indicate that dingoes diverged and have been genomically isolated from other *Canis* lineages, including wolves and domestic dogs, for 8000–11,000 years ([Table 1](#); [Cairns and Wilton 2016](#); [Bergström *et al.* 2020](#); [Zhang *et al.* 2020](#); [Bergström *et al.* 2022](#); [Souilmi *et al.* 2024](#); [Weeks *et al.* 2024](#)). Carbon dating of archaeological dingo remains from southwestern Australia indicates that they have been widespread across Australia for at least 3500 years ([Table 1](#); [Balme *et al.* 2018](#)).

High levels of genetic sharing between dingoes and Japanese wolves ([Gojobori *et al.* 2024](#)) suggest that the dingo’s ancestor may have been an Asiatic wolf, however ancient DNA studies with broader sampling of Asiatic wolves are needed to confirm this. A strict biological species concept interpretation of canid taxonomy is problematic due to the widespread occurrence of admixture, which may be evolutionarily adaptive, between *Canis* lineages ([Gopalakrishnan *et al.* 2018](#); [Schweizer 2018](#); [Smith *et al.* 2019](#); [vonHoldt and Aardema 2020](#); [Pilot 2021](#)). However, whilst many *Canis* species, including jackals (*Canis* spp.), coyotes (*Canis latrans*) and wolves (*Canis* spp.) remain biologically compatible, behavioural and geographic barriers to reproduction act to minimise gene flow between species (or subspecies) and maintain effective reproductive isolation. In this context complete reproductive isolation is not expected to be present between *Canis* species that carry the same chromosome complement.

Table 1. Summary of archaeological, morphological and genetic evidence for the timing and origin of dingoes in Australia.

Category	Source	Data type	Method/approach	Estimated divergence time (years BP)	Estimated arrival in Australia (years BP)	Key findings
Archaeological evidence	Balme et al. (2018)	Fossil (dingo bone remains)	Direct Accelerator Mass Spectrometry (AMS) radiocarbon dating from Madura Cave	–	3348–3081	Provides the oldest directly dated dingo remains; firm lower boundary for dingo arrival
Morphological evidence	Koungoulos et al. (2024)	Morphology (crania + postcrania)	3D geometric morphometrics + direct AMS dating	–	3000–3300	Shows early southeastern dingoes had smaller builds and closer cranial affinity to East Asian and New Guinea Singing Dogs (NGSD); evidence of early regional variation
Genetic evidence – mitochondrial DNA	Savolainen et al. (2004)	mtDNA (control region)	Sequencing + phylogenetic distance to founder haplotype A29	-5000 (range 4600–10,800)	-5000 (same range used as proxy)	All dingo mtDNA types cluster around A29; suggests a single introduction event and small founder population from East Asia
	Oskarsson et al. (2012)	mtDNA (control region)	Broader analysis of SE Asian, Polynesian, and Australian dogs	-4600–18,300	-4000–8000 (implied by mtDNA spread and diversity)	Identifies route through Mainland Southeast Asia; dingo haplotype diversity suggests older introduction than archaeological record alone. Dingo haplotypes are absent from Taiwan and the Philippines, suggesting a mainland Southeast Asia route, not Austronesian expansion
	Cairns and Wilton (2016)	Whole mtDNA +13 nuclear loci	Bayesian divergence time estimation	-8300	6000–10,000	Finds evidence of two distinct dingo populations; plausible multiple introductions and regional structuring
	Zhang et al. (2020)	Whole genome + mtDNA	Phylogenetics + demographic modelling	-8300	–	Indicates divergence from southern East Asian dogs; identifies selection in dietary and behavioural genes related to wild living
Genetic evidence – genome-wide	Kumar et al. (2023)	Whole genome	Genomic diversity, runs of homozygosity (ROH), deleterious load	-4000–11,000	–	Finds strong founder effects and lowest diversity among canids; supports ancient colonisation and long isolation

(Continued on next page)

Table 1. (Continued)

Category	Source	Data type	Method/approach	Estimated divergence time (years BP)	Estimated arrival in Australia (years BP)	Key findings
Genetic evidence – ancient DNA	Souilmi et al. (2024)	Ancient and modern genome-wide	mtDNA, nuclear DNA, demographic modelling	mtDNA ancestor -3000–8000	Ancient samples: 400–2746	Demonstrates deep population structure already existed thousands of years ago; confirms continuity and minimal post-colonial admixture
Synthesis and interpretive reviews	Fillios and Taçon (2016)	Genetic + archaeological evidence (from prior studies)	Critical synthesis of archaeological and genetic data	–	3500–10,000	Integrates multiple data types; proposes Sulawesi as parsimonious origin; supports early, possibly multiple arrivals
	Smith et al. (2019)	Integrative review (fossil, genetic, morphological, behavioural)	Critical synthesis of archaeological, molecular, phenotypic, ecological and taxonomic data	-5000–10,000	3500–10,000	Reviews multiple lines of evidence supporting dingo divergence from East Asian dogs prior to agriculture. Affirms arrival in Australia at least 3500 years ago, likely between 5000–10,000 BP. Suggests arrival was independent of Neolithic cultural markers, possibly with hunter-gatherers. Highlights long isolation from other canids post-arrival
	Cairns (2021)	Genome-wide single nucleotide polymorphism (SNP) data (from prior studies); functional gene analysis (e.g. AMY2B)	Review and reinterpretation of existing genomic data; emphasis on functional traits and divergence context	-8000–10,000	≥3500	Argues dingoes diverged from domestic dogs before the rise of agriculture; highlights AMY2B deletion (lack of starch adaptation); supports early, non-Neolithic separation and long isolation from other dogs

Note: some genome-wide studies estimate dingo divergence from other dog lineages at 8000–11,000 BP (e.g. [Zhang et al. 2020](#); [Kumar et al. 2023](#)), while archaeological evidence supports arrival in Australia at least -3500–4000 BP ([Balme et al. 2018](#)). It is possible that genetic divergence occurred prior to arrival and in Southeast Asia or near Oceania, not within Australia.

There have been significant changes to our knowledge about the genetic identity of dingoes and patterns of inter-specific hybridisation with domestic dogs. Cairns *et al.* (2023) demonstrated that there is limited contemporary interbreeding between dingoes and domestic dogs across the Australian landscape, revealing effective reproductive isolation between the lineages. Weeks *et al.* (2024) corroborated the finding of limited contemporary gene flow between dingoes and modern domestic dogs, especially in Victoria. Additionally, Kreplins *et al.* (2024) showed little dingo introgression in Aboriginal community dogs in remote Western Australia, even though the dingoes and domestic dogs lived in close proximity. Ancient DNA studies have confirmed the divergent pre-historic and present-day identity of dingoes in Oceania from modern domestic dogs (Souilmi *et al.* 2024; Scarsbrook *et al.* In Press). While Scarsbrook *et al.* (In Press) report historical gene flow (1800s–1960s) from domestic dogs into southeastern dingoes, they find evidence that dog alleles retained in contemporary dingoes have been positively selected and may have played a role in mitigating inbreeding depression. Together these studies highlight that contemporary dingo populations have maintained their evolutionary distinctiveness from domestic dogs, with limited present-day gene flow between the lineages.

There are several mechanisms possibly driving reproductive isolation between dingoes and modern domestic dog lineages in Australia. There is limited opportunity for dingoes and domestic dogs to interact with over 85% of the human (and domestic dog) population residing in urban areas/capital cities within 50 km of the coast (Australian Bureau of Statistics 2020). Further, around 80% of pet domestic dogs in Australia are neutered (Animal Medicines Australia 2019), limiting opportunity for reproduction between dingoes and domestic dogs. There are also key differences in the reproductive strategies of dingoes (seasonal breeding and biparental care) and domestic dog lineages (non-seasonal breeding and uniparental care) (Lord *et al.* 2013; Cursino *et al.* 2017). As such, female dingoes are only able to conceive during a short window, limiting the opportunity for hybridisation. Furthermore, strong social behaviours, such as the maintenance of cohesive family pack structures and territories (Thomson *et al.* 1992), reduces the likelihood of mating between an established dingo family and interloping dogs.

One key point of difference between dingoes and domestic dogs is that dingoes can live independently in the wild. The absence of wild domestic dog populations in Australia (Stephens *et al.* 2015; Cairns *et al.* 2021; Stephens *et al.* 2022) suggests that modern domestic dogs are not capable of living independently, forming self-sustaining populations in the wild or establishing themselves within the pack structure of dingoes; which may be driven by an inability to meet their own energetic needs or reproduce successfully. This inability of domestic dogs to establish populations in the wild is made particularly apparent by the absence of wild dog populations in Tasmania and New Zealand (Letnic *et al.* 2012; King and

Forsyth 2021). Both of these islands support a similar range of dog breeds and land-management strategies to mainland Australia, but both lack wild dogs. The best explanation for the presence of dingoes on mainland Australia and the absence of wild domestic dogs across mainland Australia, Tasmania and New Zealand is that dingoes and their hybrids have the genetic material necessary to live in the wild but domestic dogs do not. The inability to self-sustain in Australian ecosystems reproductively isolates domestic dogs from dingoes and highlights that while domestic dogs are obligate synanthropes, dingoes are not (Lord *et al.* 2025). Reproductive isolation between dingoes and domestic dogs may be partly due to pre-zygotic behavioural barriers as well as posited differences in ecological and reproductive fitness (Letnic *et al.* 2012; Ballard and Wilson 2019; King and Forsyth 2021).

Criterion 2: evidence that dingoes are genetically distinct from domestic dog breeds

Genomic studies find evidence of at least three lineages of dog that diverged from ancestral wolf populations: eastern dogs, arctic dogs and western dogs (Frantz *et al.* 2016; Bergström *et al.* 2020, 2022; Feuerborn *et al.* 2021; Perri *et al.* 2021; Gojobori *et al.* 2024). These three early dog lineages either evolved from different wolf populations (Frantz *et al.* 2016; Freedman and Wayne 2017; Bergström *et al.* 2022) or diverged from a common protodog ancestor prior to the rise of agriculture and the initiation of intensive domestication processes (Arendt *et al.* 2016; Bergström *et al.* 2020; Zhang *et al.* 2020; Cairns 2021; Perri *et al.* 2021; Field *et al.* 2022; Gojobori *et al.* 2024).

Dingoes are a wild-living canid descended from the eastern dog lineage whilst extant modern domestic dogs primarily originate from the western and Arctic dog lineages (Fig. 2; Bergström *et al.* 2020, 2022; Gojobori *et al.* 2024). While village dogs found in Asia today carry ancestry from the eastern dog lineage, they have experienced ongoing gene flow from western dog lineages over the last few thousand years (Fig. 2; Pilot *et al.* 2015; Shannon *et al.* 2015; Bergström *et al.* 2020; Surbakti *et al.* 2020; Ahn *et al.* 2023; Gojobori *et al.* 2024). Both ancient and modern western dogs are more closely related to the Arctic dog lineage than to eastern dogs, including the dingo (Bergström *et al.* 2020; Surbakti *et al.* 2020; Feuerborn *et al.* 2021; Perri *et al.* 2021; Bergström *et al.* 2022). Modern domestic dog breeds such as the Siberian husky share ancestry with the ancient Arctic dog lineage, but they also carry ancestry from western dogs and have been selectively bred by humans over the last few thousand years (Brown *et al.* 2013; Sinding *et al.* 2020; Feuerborn *et al.* 2021; Perri *et al.* 2021). Once the ancestor of dingoes arrived in Oceania the lineage has remained isolated from other *Canis* species including domestic dogs (Ardalan *et al.* 2012; Oskarsson *et al.* 2012; Sacks *et al.* 2013; Cairns and Wilton 2016; Cairns *et al.* 2018; Greig *et al.* 2018; Zhang *et al.* 2020; Cairns 2021).

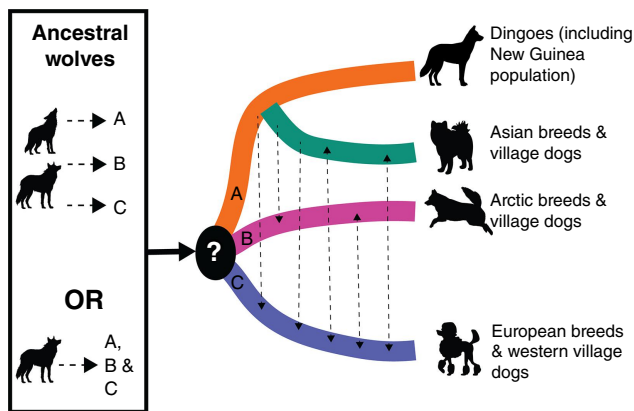


Fig. 2. Schematic of the hypothesised evolutionary origins of dogs and dingoes. Wolves are the ancestors of the first dogs, however, it is unclear whether a single or multiple wolf populations were the ancestors of early dogs. Following the divergence of dogs from wolves, there were three dog lineages, (a) the Eastern or Asian dog lineage, (b) the Arctic dog lineage and (c) the West Eurasian dog lineage. The evolutionary distinctiveness of dingoes is highlighted by an extended period of isolation in Oceania, while gene flow occurred extensively between other dog lineages across the globe during the last 10,000 years, as depicted by dashed black lines. Figure drawn in Adobe Illustrator 2025 based on our current knowledge of the evolutionary origins of dingoes and dogs including the work of Pilot *et al.* (2015), Shannon *et al.* (2015), Parker *et al.* (2017), Bergström *et al.* (2020), Surbakti *et al.* (2020), Zhang *et al.* (2020), Cairns (2021), Bergström *et al.* (2022), Cairns *et al.* (2023), Gojobori *et al.* (2024).

Ancient DNA studies have corroborated the distinctiveness of modern and ancient dingoes from extant domestic dogs (Fig. 3; Souilmi *et al.* 2024). Genome-wide marker studies have demonstrated strong evidence of genetic differentiation between dingoes, domestic dogs and wolves (Fig. 3; Cairns *et al.* 2023; Weeks *et al.* 2024). Cairns *et al.* (2023) reported high levels of genetic differentiation between dingoes and domestic dogs, with calculated Fixation Index (FST) values exceeding 0.25. Genomic comparisons between dingoes, domestic dogs and wolves have identified evidence of evolutionary change since their arrival in Australia (Zhang *et al.* 2020; Field *et al.* 2022). Field *et al.* (2022) reported the presence of structural chromosomal differences (inversions and duplications) between wolves, dingoes and domestic dogs. Furthermore, genomic studies found that dingoes were not subjected to the same intensive selective breeding and dietary modifications as the ancestors of modern domestic dog breeds (Arendt *et al.* 2016; Zhang *et al.* 2020; Field *et al.* 2022).

Criterion 3: evidence that dingoes form an independently derived evolutionary lineage that is more distinct from domestic dog breeds than dog breeds are from each other

The direct ancestors and processes underlying the origins of early dogs remain unclear, including whether there was a

single or multiple ancestral wolf populations (Freedman and Wayne 2017; Bergström *et al.* 2020; Perri *et al.* 2021; Bergström *et al.* 2022; Gojobori *et al.* 2024). However, there is a wide range of morphological and physiological evidence that dingoes are distinct from domestic dog lineages and are more divergent from domestic dog lineages than breeds are from each other (Crowther *et al.* 2014; Smith *et al.* 2019; Cairns 2021; Smith *et al.* 2023). Modern genomic evidence confirms the distinctiveness of modern dingoes from extant domestic dogs (Bergström *et al.* 2020; Surbakti *et al.* 2020; Zhang *et al.* 2020; Cairns 2021; Field *et al.* 2022; Cairns *et al.* 2023; Gojobori *et al.* 2024). Both modern and ancient dingoes (including the New Guinea Singing Dog (NGSD)) form a distinct genetic cluster to wolves as well as domestic dogs (Fig. 3).

Dingoes, including the NGSD, are an example of the eastern dog lineage which diverged early and has remained free from admixture with other wild canids or dog lineages (Bergström *et al.* 2020; Surbakti *et al.* 2020; Gojobori *et al.* 2024). The ancestry of extant domestic dogs is complex due to historical admixture and migration across the globe as well as the actions of humans in selective breeding (Gopalakrishnan *et al.* 2018; Bergström *et al.* 2022). Extant domestic dog breeds and village dog populations in Eurasia, Europe, Africa and the Americas descend almost exclusively from the western dog lineage or from admixture between various dog lineages (Pilot *et al.* 2015; Shannon *et al.* 2015; Bergström *et al.* 2020; Surbakti *et al.* 2020). Furthermore, most extant domestic dog breeds were only developed in the last 200–400 years and are genetically shallow lineages (Parker *et al.* 2017). Based on this genomic evidence, dingoes represent an evolutionary lineage that is independent and discrete from extant domestic dogs and has been so for thousands of years.

Some authors argue that because the ancestor of dingoes are likely to have been transported to Oceania by humans, then they are a domesticate and are not evolutionarily independent from domestic dogs (Jackson *et al.* 2017; Jackson *et al.* 2019; Jackson *et al.* 2020). However, humans have transported many animal lineages around the globe and these lineages are not considered domesticates, according to conventional definitions of domestication (Heinsohn 2014; Ahlgren *et al.* 2016; Hofman and Rick 2018; Lord *et al.* 2025). Good examples of this are rusa deer (*Cervus timorensis*) and Malay civets (*Viverra zibetha*), which are believed to have been transported by humans across Wallace's line during the last 5000–10,000 years (Veron *et al.* 2014; Martins *et al.* 2018). Like dingoes in Australia, rusa deer and Malay civets live in the wild on numerous islands and are not considered to be a domesticate.

Further evidence that dingoes are a distinct lineage from domestic dogs is their lack of AMY2B copy number variation, which is a dietary adaptation observed in ancient and modern domestic dogs associated with prehistoric agricultural expansion (Arendt *et al.* 2016). The dingo lineage diverged from its ancestors roughly 8000–11,000 years ago

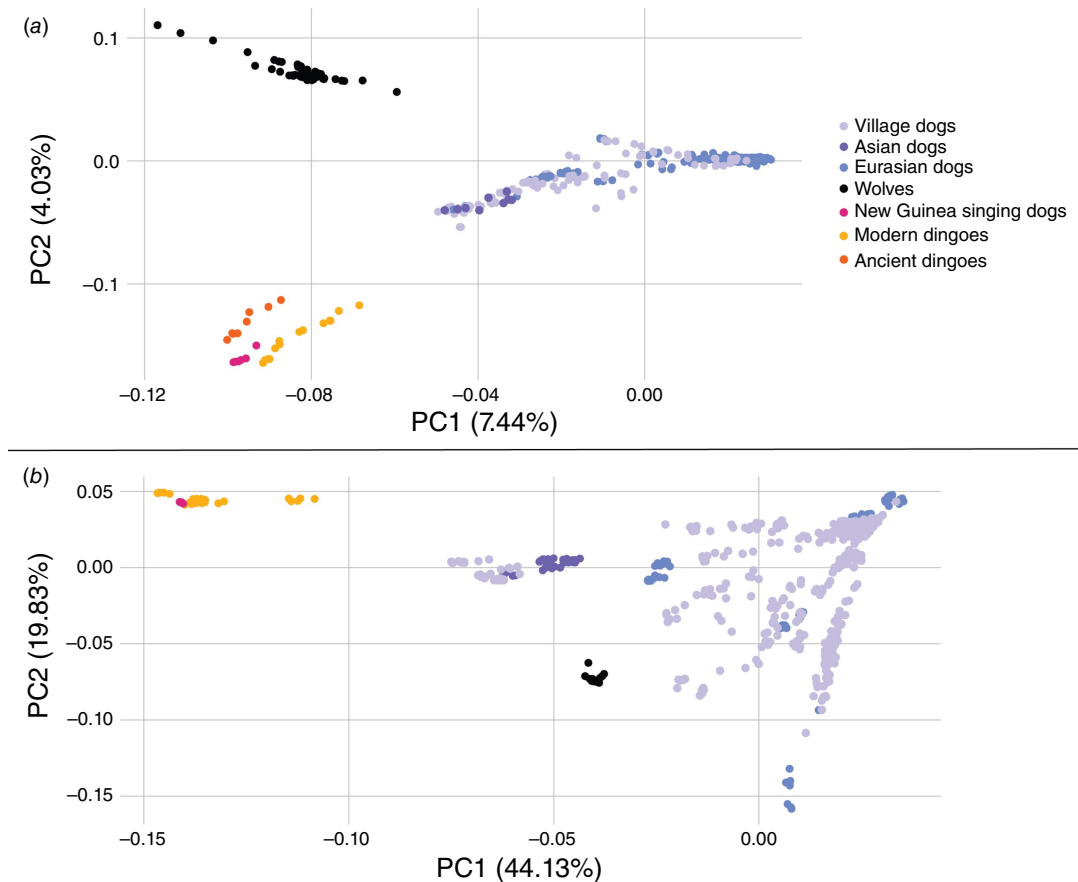


Fig. 3. (a) Principal Component Analysis (PCA) based on nuclear genomic data of dingoes (modern and ancient), New Guinea singing dogs, wolves and global domestic dog populations. The PCA has been re-plotted in R using ggplot2 and SMARTPCA analysis from Souilmi *et al.* (2024). Note that we have excluded two ancient dingo samples from Souilmi *et al.* (2024), one that was sequenced using a domestic dog bait capture method and one which had extremely low coverage ($<0.01\times$). (b) PCA from Cairns (2021) based upon filtered Illumina genome wide Single Nucleotide Polymorphism (SNP) data (113,523 sites) from 657 canid samples including wolves, dingoes, New Guinea singing dogs and global dog populations, replotted in R using ggplot2.

(Cairns and Wilton 2016; Bergström *et al.* 2020; Zhang *et al.* 2020; Souilmi *et al.* 2024), which was likely prior to the intensification of the human-canine relationship, particularly human control of canine reproduction and selective breeding. Studies of Y-chromosome and mitochondrial DNA indicate that dingoes reflect an different older migration event than the ancestors of dogs in Island South East Asia and the Pacific (Sacks *et al.* 2013; Greig *et al.* 2018). Thus, in our opinion it is erroneous to label all dog lineages as domesticates when not all dog lineages had, or were posited to have, a relationship with humans that falls within domestication criteria (Fig. 1; Manwell and Baker 1984; Galibert *et al.* 2011; Zeder 2012; Larson and Burger 2013; Smith *et al.* 2019; Cairns 2021; Purugganan 2022; Smith *et al.* 2023). Whilst early dogs and the ancestor of dingoes may have been commensal or anthrophilic, in Oceania dingoes live (or lived) free from human interaction or control. We know that some dingoes lived with or in close association to Indigenous Australians (Smith and Litchfield 2009; Kounigoulos and Fillios 2020;

Kounigoulos 2021), but it is unclear what evolutionary impact this had on free-living dingoes as a population.

Criterion 4: relationship of dingoes to dogs from south east Asia

It has been commonly postulated that village dogs in south east Asia with phenotypic similarity to dingoes are either the direct progenitors of dingoes, or are dingoes themselves (Corbett 2001). However, modern genomic evidence has illustrated that dingoes are distinct from extant Asian village dogs (Fig. 3; Surbakti *et al.* 2020; Field *et al.* 2022; Cairns *et al.* 2023; Kumar *et al.* 2023; Gojobori *et al.* 2024; Souilmi *et al.* 2024). Indeed, Ahn *et al.* (2023) found that dingoes (and NGSD) form a distinct population to Asian village dogs and exhibit F_{ST} values of >0.25 , similar to the F_{ST} values observed between wolves and Asian village dogs.

Extant Asian village dogs are a heavily admixed lineage, carrying small amounts of persisting eastern dog lineage, as

well as significant ancestry from western and modern domestic dog lineages from recurring admixture over the last several thousand years (Fig. 2; Pilot *et al.* 2015; Shannon *et al.* 2015; Bergström *et al.* 2020; Surbakti *et al.* 2020; Ahn *et al.* 2023; Gojobori *et al.* 2024). Scientists should be cautious in interpreting phylogenetic analyses depicting Asian village dogs or breeds as basal to dingoes because many phylogenetic methods inadequately account for patterns of ancient, historical and modern admixture (Surbakti *et al.* 2020; Bergström *et al.* 2022). It is indisputable that dingoes and early Asian dogs share ancestors; however, the evolutionary trajectory of dingoes has diverged due to adaptation to Australian environments and isolation from other wild or domestic canids. Asian dogs, on the other hand, have continued along a domestication trajectory, living in close proximity to humans (obligate synanthropes) and experiencing persistent genetic swamping from Western dogs.

Conclusions

Significant advances in genomic research provide robust evidence that dingoes are on a biologically meaningful and divergent evolutionary trajectory from both domestic dogs and extant populations of wolves. Our existing knowledge of morphological and biological differentiation between dingoes, wolves and domestic dogs (Crowther *et al.* 2014; Smith *et al.* 2019), along with the new evidence of reproductive isolation (Cairns *et al.* 2023; Weeks *et al.* 2024), highlights the need for a reconsideration of the taxonomic status and nomenclature used for dingoes. We disagree with the interpretation of some authors that any association with humans or domestication pressure (passive or active), at any time point, precludes lineages from nomenclatural distinction (Jackson *et al.* 2017; Gaunitz *et al.* 2018; Jackson *et al.* 2019; Jackson *et al.* 2020). This interpretation is problematic because it precludes any anthropophilic or commensal lineage from being defined as a species, no matter how distinct the lineage has become or how long the lineage has been distinct.

When considering how we make these distinctions it is also imperative to consider the cultural context, acknowledging traditional knowledge about the identity of species and relationships between a species and humans. In the case of dingoes, human-dingo relationships are sacred, and dingoes prominently feature in the Law/Lore of Indigenous Australians, as well as being a part of the network of relationships in Country. We argue that for ongoing discussions about the nomenclature or taxonomy of species where humans may have played a role, it is important that researchers properly define the human-animal relationship (i.e. domestication), as well as highlighting the relative impact and extent of human selection on the lineage to the exclusion of natural forces (Fig. 1).

We concur with Gentry *et al.* (2004) that nomenclatural differentiation between domestic and wild lineages should

be adopted to provide clarity to legislators, wildlife managers and applied scientists (conservation, ecology, behaviour etc.). There are several ways that taxonomic nomenclature rules and conventions can be applied to dingoes. It is clear from their historical treatment and emerging genomic evidence that dingoes represent a distinct taxonomic unit to domestic dogs, what is less clear is whether dogs, including both dingoes and domestic dogs, are a discrete species from wolves. If it is agreed that dogs are a discrete species from wolves and accepting ICZN Opinion 2027 that wild and domestic lineages should have distinct nomenclature, we could utilise *Canis dingo* for the dingo lineage and *Canis familiaris* to refer to domestic lineage(s) of dogs. An alternative approach utilising trinomial nomenclature would be to nominate nomenclature for the original protodog(s) and then designate dingoes and domestic dogs as subspecies of that dog lineage. Either of these solutions allows taxonomic end-users to unambiguously distinguish between distinct evolutionary lineages of dog – one which is a valid wild taxon and the other which is a domestic complex. These approaches acknowledge the shared evolutionary history of these lineages, their differentiation from wolves and the divergent evolutionary trajectories of dingoes and domestic dogs. If the taxonomic differentiation of dogs from wolves is considered unclear then an alternative solution would be to continue including dingoes and dogs under *Canis lupus*, referring to the distinct evolutionary lineages as *Canis lupus dingo* and *Canis lupus familiaris*. We contend that a binomial or trinomial variant of *Canis familiaris* should not be applied to dingoes given this nomenclature refers specifically to modern domestic dogs.

Conservation implications of taxonomic uncertainty for dingoes

The taxonomic treatment and nomenclature of dingoes is not simply philosophical but has ‘real world’ practical implications in terms of conservation and management. While the Australian Mammal Taxonomy Consortium argues that ‘naming the dingo as a separate species should not be necessary to protect it ...’, the reality is that if a lineage is not considered taxonomically discrete at either the species or subspecies level then legislative protection is difficult. Indeed, the New South Wales (NSW) Threatened Species Scientific Committee decided in May 2024 that due to the Australian Faunal Directory listing dingoes as *Canis familiaris*, ‘the dingo is not eligible for listing under the Act as it is not recognised as a defined subspecies’ (NSW Threatened Species Scientific Committee, pers. comm.). This difficulty is based on the assessment that if dingoes share the nomenclature *Canis familiaris* with domestic dogs, then they are not evolutionarily or taxonomically distinct, and as such would not warrant specific conservation management. This also has implications for the status of dingoes, and plausibly domestic dogs, as a native animal under Australian legislation. Currently, the federal government and most states classify dingoes legislatively as

a native animal based on their presence in Australia prior to 1400 AD (or prior to 1788), but if dingoes and domestic dogs are not taxonomically discrete then this may also unintentionally include domestic dogs.

Conversely, taxonomic treatment of dingoes as *Canis lupus dingo* or *Canis dingo* allows jurisdictions to distinguish between evolutionarily distinct dingoes and domestic dogs under legislation (and in public policy), thus practically enabling different conservation and management policies for dingoes and domestic dogs. This differentiation also would not inappropriately include dingoes in companion animal legislation. Furthermore, taxonomic treatment of dingoes as either a species or subspecies would allow appropriate acknowledgement and management of the dingo as a ‘culturally significant species/entity’ (Goolmeier *et al.* 2022) without inappropriately including domestic dogs.

Next steps

It is unlikely that debate about the taxonomy and nomenclature of dingoes will be resolved by ongoing academic debate in the literature. The ICZN (1999) specifically notes in the Code’s introduction that (1) ‘the Code refrains from infringing upon taxonomic judgment ...’ and (2) ‘nomenclature does not determine the inclusiveness or exclusiveness of any taxon ... but rather provides the name that is to be used for a taxon whatever taxonomic limits and rank are given to it’. There is academic freedom in how scientists define species, how species are distinguished from subspecies and how nomenclature is applied to taxonomy (Gentry *et al.* 2004; De Queiroz 2007; Clutton-Brock 2015; Thiele *et al.* 2021). However, for end-users, and those outside of, or not versed in the nuances of academic debate, ongoing taxonomic debate results in instability (Coates *et al.* 2018). Any proposal to seek consensus on the naming of dingoes needs to engage in broad consultation with taxonomists, taxon specific experts as well as seeking feedback from both Australian and international scientific organisations, and representatives of First Nations, to inform nomenclature decisions; i.e. the International Union for the Conservation of Nature (IUCN) Canid Specialist Group and the Australian Mammal Society. Scientists communicating with policy makers and wildlife managers should ensure that decisions about taxonomic nomenclature are transparent, evidence-based and presented as scientific hypotheses with alternative views acknowledged. We further propose an approach similar to that employed by the United States National Academies of Sciences, Engineering and Medicine where a comprehensive, independent and evidence-based review of the taxonomic status of red wolves (*Canis rufus*) and Mexican wolves (*Canis lupus baileyi*) was undertaken including consultation with taxonomic experts and wolf experts with diverse opinions (National Academies of Sciences, Engineering, and Medicine 2019). Given significant scientific progress in recent years, and the implications for public

policy, we aim to advance this discussion and advocate for an independent review of the taxonomic status and nomenclature of dingoes by an appropriate Australian institution such as the Australian Academy of Science.

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Data availability. All data are provided within this paper or the relevant cited literature.

Conflicts of interest. K. M. C. is co-coordinator of the IUCN Species Survival Commission (SSC) Canid Specialist Group's Dingo Working Group and a voluntary scientific advisor to the Australian Dingo Foundation and New Guinea Highland Wild Dog Foundation. B. P. S. is a member of the IUCN SSC Canid Specialist Group's Dingo Working Group and a non-financial director of the Australian Dingo Foundation. The other authors declare no conflicts of interest.

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